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河北丰宁早期鲟类化石一新属

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摘要 发现于河北丰宁晚侏罗或早白垩世义县组的燕鲟以其很长的背鳍、长条形的方颧骨、骨化程度较高的中轴骨骼和支鳍骨、鳍条上残留有硬鳞质、无轴上鳍条等，有别于鲟形目所有已知属。燕鲟的吻部骨骼退化为管状小骨片，下鳃盖骨前方明显呈舌状突出，后部裂成锯齿状，尾鳍上硬鳞退化，与列鳍鱼和北票鲟最为相近，暂可归入北票鲟科；北票鲟科的鳃条骨数目少于7根，尾鳍上硬鳞无关节突和凹，可视为鲟亚目(鲟科＋匙吻鲟科)的近祖姊妹群。热河群义县组和九佛堂组应为同期异相沉积，且沉积速度很快。

关键词 河北丰宁，晚侏罗或早白垩世，鲟类化石

北票鲟 (*Peipiaosteus* Liu et Zhou 1965) 多年来一直为我国唯一的鲟类化石代表。进入九十年代以来，随着有关热河动物群专题研究工作的开展，发现并记述了属于匙吻鲟科的早期化石材料(周忠和 1992，卢立伍 1994)。河北区调所在从事"全国多重地层划分——地层清理"工作中，在河北北部丰宁一带又发现了一种新的鲟类化石。至此，在冀北辽西热河群的地层中发现的鲟类化石已有3个属4个种，分属2个科。这批化石属种对了解鲟形鱼类在晚侏罗—早白垩世这一承前启后阶段的发展演变史具有重要的意义。

文中对河北区调所发现的新材料做了系统描述，依据其很长的背鳍等明显有别于鲟类已知属种的特征，建立了一新属新种。同时分析讨论了鲟类，尤其是早期化石类群的研究现状；并初步认为燕鲟与列鳍鱼和北票鲟最为相近，北票鲟科则可视为鲟科和匙吻鲟科的近祖姊妹群。文中对热河群义县组和九佛堂组的对比及沉积速率等提出了一点新认识。

一、系统描述

鲟形目 Acipenseriformes Berg, 1940

北票鲟科 Peipiaosteidae Liu et Zhou, 1965

燕鲟属(新属) *Yanosteus* gen. nov.

属型种 长背鳍燕鲟 *Yanosteus longidorsalis* gen. et sp. nov.

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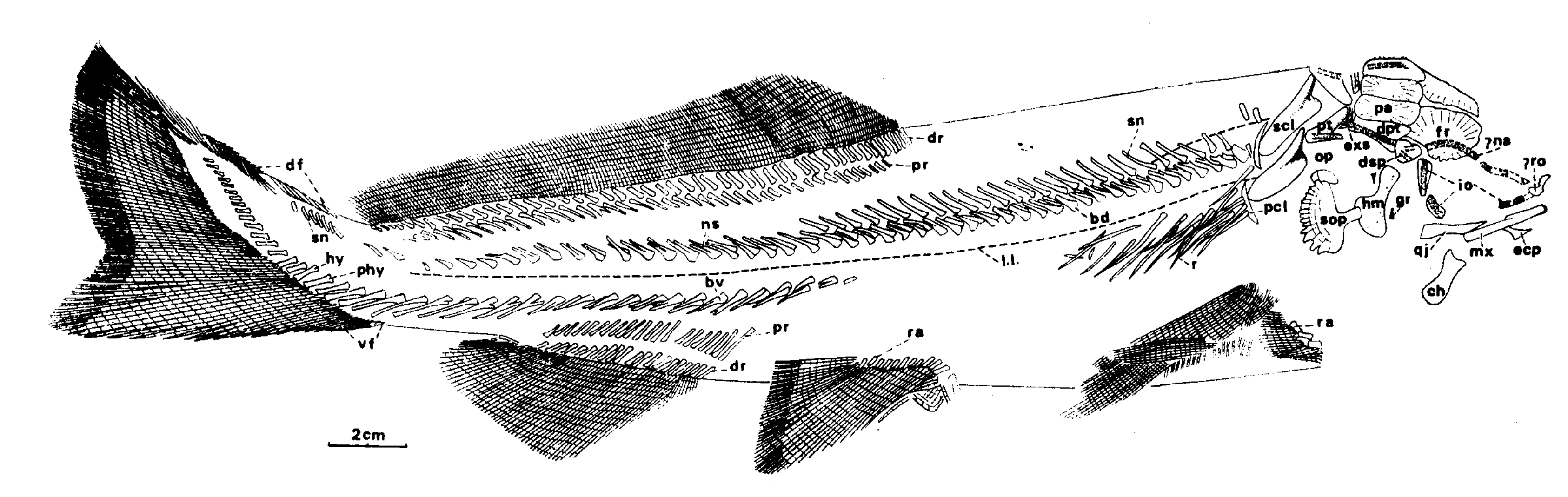


图 1　长背鳍燕鲟(新属新种)的线条图(依 V10998.2)

Fig. 1　Line drawing of *Yanosteus longidorsalis* gen. et sp. nov. (after V10998.2)

Abbreviations: bd, basidorsals; bv, basiventrals; ch, ceratohyal; df, dorsal caudal fulcra; dpt, dermopterotic; dr, distal radials of dorsal and anal fins; dsp, dermosphenoid; ecp, ectopterygoid or ectopterygoid process of maxilla; exs, extrascapular; fr, frontal; gr, gill rakers; hm, hyomandibular; hy, hypurals; io, infraorbital bones or tube-like bones enclosing infraorbital sensory canal; mx, maxilla; na, nasal; ns, neural spines; op, opercle; pa, parietal; pcl, postcleithrum; phy, parhypural; pr, proximal radials of dorsal and anal fins; pt, posttemporal; qj, quadratojugal; r, pleural ribs; ra, radials of pectoral and pelvic fins; ro, rostral; scl, supracleithrum; sn, supraneurals; sop, subopercle; vf, ventral caudal fulcra; l.l., lateral line

属征　燕鲟以其很长的背鳍（背鳍基长可达全长的 1/3 左右）显著有别于鲟形鱼类所有已知属。此外，燕鲟尚具有下列鉴定特征：腭骨已骨化；方颧骨长条形，前端尖；眶上和眶下感觉管在膜质蝶耳骨相连；椎体弓片、上神经棘、肋骨及各鳍支鳍骨的骨化程度高；鳍条上残留有硬鳞质；尾鳍无轴上鳍条；尾下叶基部有数对未愈合的棘鳞。

词源　Yan-取自化石产地河北北部的简称"燕"；-osteus 来自希腊文"osteon"，意为骨，鲟类化石的属名多引用该词根。

长背鳍燕鲟（新属新种）*Yanosteus longidorsalis* gen. et sp. nov.

（图 1—2；图版 I-II）

正型标本　一基本完整的个体。古脊椎动物与古人类研究所标本登记号：V10998.1。

标本　两条基本完整的鱼（V 10998.2—3），两个不完整的头骨及一块尾部标本（V10998.4—6）。

种征　同属征。头长约为全长的 1/5；胸、腹鳍鳍条约 40 根，背鳍条约 170 根，臀鳍条 50 余根，尾鳍条 80 余根；尾鳍上叶背缘有 20 余对背棘鳞，下叶基部有 4—6 对腹棘鳞；尾部硬鳞限于尾上叶后上角，无关节突和凹。

产地和层位　河北省丰宁县森吉图乡东土窑；晚侏罗或早白垩世义县组。

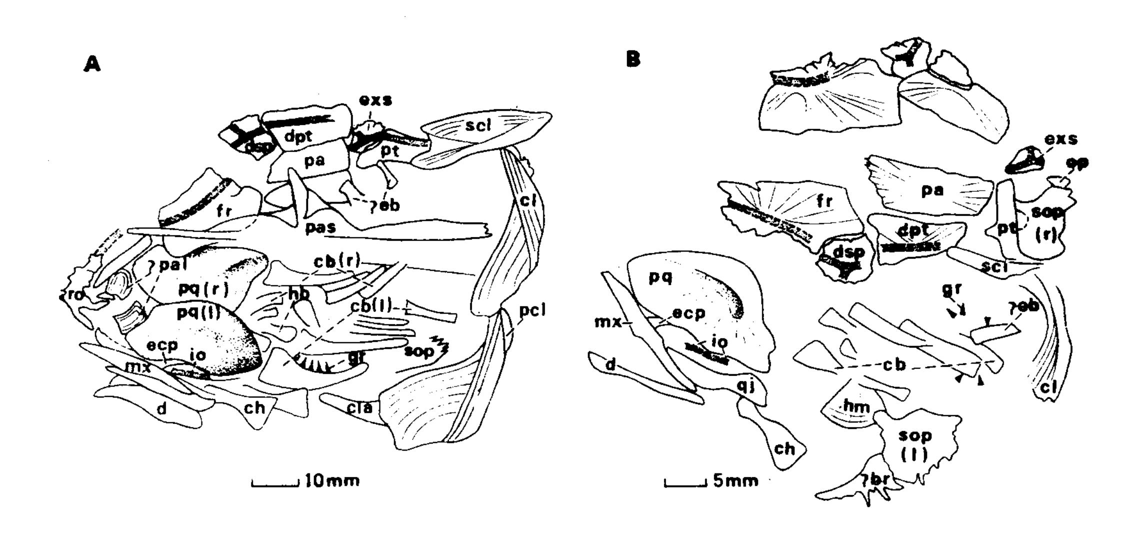


图 2　长背鳍燕鲟（新属新种）的头骨

A）正型标本 V10998.1 的头骨背一侧视；　B）V10998.5 号标本头骨背一侧视

Fig. 2　Skull of *Yanosteus longidorsalis* gen. et sp. nov.

Line drawings of holotype V10998.1 (A) and V10998.5 (B) in dorso-lateral view. Abbreviations:br, branchiostegals; cb, ceratobranchials; cl, cleithrum; cla, clavicle; d, dentary; eb, epibranchials; hb, hypobranchials; pal, palatine; pas, parasphenoid; pq, palatoquadrate; see Fig. 1 for other abbreviations. (l) and (r) indicate left and right

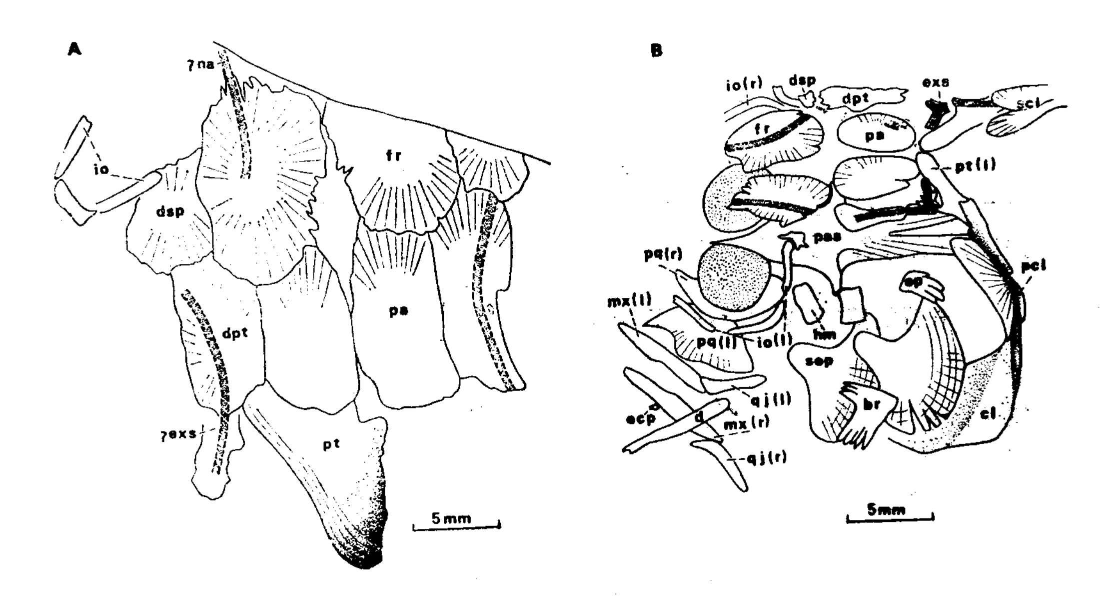


图 3 潘氏北票鲟的头骨

A) 部分颅顶骨片(依 V3049.3); B) 头骨背一侧视线条图(依 V9474.26A—B)

Fig. 3 Skull of *Peipiaosteus pani* Liu et Zhou, 1965

A) Line drawing of skull roof of V3049.3; B) Line drawing of skull in dorso-lateral view, mainly based on V9474.26A, but parasphenoid, jaws and postcleithrum reversed from V9474.26B. Both specimens are from the Late Jurassic or Early Cretaceous Yixian Formation at Jianshanzigou, Beipiao City, Liaoning Province

词源 Longi-取自拉丁文 "longus"; -dorsalis 来自现代拉丁文 "dorsalis"。种名表示这种鱼所具有的长背鳍特征。

描述 本文记述的六件标本均较大，三个基本完整个体的全长分别为 454 mm (V 10998.1), 394 mm (V 10998.2) 和 334 mm (V 10998.3); 一头 (V 10998.4) 一尾 (V10998.6) 所代表的两个个体的全长不小于 460mm; 另一较小的头骨 (V10998.5) 代表了现有标本中最小的个体，估计全长仍可达 270 mm 左右。所有标本的骨骼骨化程度均较高，膜质骨和鳍条被有硬鳞质层 (ganoine)。

现有标本中，头骨均以背一侧压状态保存，这表明燕鲟的体型与软骨硬鳞鱼 (*Chondrosteus* Egerton) 的较为相似，而不似北票鲟 (*Peipiaosteus* Liu et Zhou) 和现生鲟类那样身体腹面扁平且宽大，北票鲟的头骨多以背一腹压保存。

头骨——燕鲟的头部较短，自吻端至下鳃盖骨后缘的头长仅约为全长的 1/5 (图版 I, II 1)。

颅顶骨骼在各标本上保存完好，包括额骨 (frontal)、顶骨 (parietal)、膜质蝶耳骨 (dermosphenoid)、膜质翼耳骨 (dermopterotic)、额外肩胛骨 (extrascapular) 和后颞骨 (posttemporal) (图 1—2)，其形态特征与北票鲟和软骨硬鳞鱼较相似(图 3, Traquair 1887)。额骨在颅顶骨骼中最为长大，其长略大于顶骨，宽几达顶骨与翼耳骨宽之和。顶

骨与翼耳骨近长方形，二者大小相若。左右额骨和顶骨间以直线相接，但额、顶骨间以锯齿状边缘嵌接。膜质蝶耳骨与额骨后外侧缘及翼耳骨前外侧缘相接，眶上、眶下和眶后感觉管汇合于此骨（V10998.4）。额外肩胛骨为一近三角形的小骨片，其上有横枕管通过。后颞骨叉状，但腹枝相对背枝极为窄小，多不易保存和辨认。刘宪亭和周家健(1965)曾把北票鲟的后颞骨记述为"一长条形的骨片"（V3049.3）；周忠和(1992：图 3)则将其误认为上匙骨的上段。除上述六对骨片外，自额骨前侧缘至吻端常保存有一列管状骨片，形状不规则，据其位置和有感觉管分布，推测应包括鼻骨（nasal）和吻骨（rostral）在内（图 1、2A，图版 II 1)。

脑颅腹面的副蝶骨（parasphenoid）宽大，前部呈宽舌状，腹面沿中轴略凸出，后部往后分成两叉，中部向两侧伸出一小枝，是为上升枝（ascending ramus)。燕鲟副蝶骨的形态特征与北票鲟的基本一致(图 2A，图版 II 1、2，刘宪亭和周家健 1965：图 2A)。

围绕眼眶后、腹缘有一列管状骨片，数目约 5—6 块，其上分布有感觉管，因而当为眶下骨。

燕鲟的口下位，但吻部仅稍突出(图 1—2，图版 I、II 1)。Traquair (1887) 做的软骨硬鳞鱼的头部复原图，吻部非常突出，口完全位于吻后。Watson (1925) 对软骨硬鳞鱼的头骨重新做了复原，但吻部仍很突出。从 Woodward (1895) 和 Hennig (1925) 等文所附图版看，软骨硬鳞鱼的吻长和口的位置应与燕鲟基本相同。

颌弓主要由腭方骨（palatoquadrate)、腭骨（palatine)、外翼骨（ectopterygoid)、上颌骨（maxilla)、方颧骨（quadratojugal）和齿骨（dentary）构成（图 1—2)。燕鲟的腭方骨为一半圆形的厚大骨片，与软骨硬鳞鱼、北票鲟及列鳍鱼（*Stichopterus* Reis）的"翼骨（pterygoid)"很相似（Woodward 1895：图版 I 1、3，刘宪亭和周家健 1965：图版 II 1，Яковлев 1977：图版 XVI)。笔者认为燕鲟等早期鲟类化石的这一骨片代表未分化的软骨化骨上颌，即腭方骨，而不是 Woodward 等所指的翼骨。在正型标本的腭方骨前保存了一对小骨片，上有明显的同心生长纹，从其位置判断应为腭骨。古白鲟（*Paleopsephurus* MacAlpin）及现生鲟类的成体可见到骨化的腭骨（MacAlpin 1947，Jollie 1980，Grande & Bemis 1991)，但在软骨硬鳞鱼和北票鲟上未观察到这一骨片，Woodward (1895：图版 I 3) 所示的腭骨实相当于燕鲟的外翼骨。燕鲟的外翼骨为一钩状小骨，常与上颌骨一起保存，但不与之愈合。燕鲟的外翼骨是否相当于古白鲟及现生鲟类(除匙吻鲟 *Polyodon*)的上颌骨外翼突(ectopterygoid process of maxilla，MacAlpin 1947，Grande & Bemis 1991)尚有待肯定。燕鲟等早期鲟类化石和现生匙吻鲟类的腭方骨上均无相当于古白鲟和鲟科鱼类的腭翼骨外翼突（ectopterygoid process of palatopterygoid)。燕鲟的上颌骨和齿骨为长条形骨片，两者近等长。燕鲟的方颧骨长条形，前端尖，腹缘略内凹，中后部稍宽厚(图 1，2B)。

舌弓保存有舌颌骨（hyomandibular）和角舌骨（ceratohyal)，两者均为扁棒状骨片，上端略膨大，下端则显著膨大成扇形。鳃弓骨骼中保存了不少角鳃骨（ceratobranchials)、下鳃骨（hypobranchials）和个别上鳃骨（epibranchials)，亦呈扁棒状，其上着生有钉状鳃耙(图 1—2)。

鳃盖系统仅能观察到鳃盖骨（opercle)、下鳃盖骨（subopercle）和部分鳃条骨

(branchiostegals) 的残片(图 1、2B)。鳃盖骨很小,呈椭圆形。下鳃盖骨大，主体呈半圆形,前缘中部有一较大的舌状突起,后缘呈锯齿状，表面有同心生长纹及放射纹。鳃条骨在现有标本中均保存不好,其形状和数目难以确定。

脊柱和肋骨——脊柱由 50—55 枚脊椎构成（尾鳍部分除外)。每一躯椎仅保存一对骨化的背基片 (basidorsals);尾椎则包括背基片和腹基片 (basiventrals) 背腹两部分。除靠近尾鳍的几个脊椎外,成对的背基片及腹基片均未愈合。在现有的标本中,未见骨化的背间片 (interdorsals) 和腹间片 (interventrals)。在 V 10998.1—3 号标本的头后及胸鳍上方均保存有约 10 对骨化的肋骨 (pleural ribs) (图 1,图版 I、II 1)。

自头后至近相对于臀鳍基起点以前的椎体上方，可观察到一列骨化的上神经棘 (supraneurals), 近端与背基片末端相对但不相接，且每一上神经棘与相关椎体有一一对应关系。上神经棘在相对于臀鳍基起点之后至尾鳍起点之前的椎体上方并不发育，代之以由背基片向后背方生长而成的神经棘 (neural spines)。但是，在尾鳍上叶基部保存有 6—7 个支持背棘鳞的长形骨片，其形状和排列方向与上神经棘相同(图 1，图版 I)。因此，燕鲟上神经棘的分布状况似乎并不支持 Grande & Bemis (1991: 114 页) 鲟形鱼类自头后至尾鳍有一列连续的上神经棘的观点。

肩带与胸鳍——燕鲟的膜质肩带由上匙骨 (supracleithrum)、匙骨(cleithrum)、后匙骨 (postcleithrum) 和锁骨 (clavicle) 组成，其形态特征与北票鲟等亦十分相似 (图 1—3)。上匙骨长圆条状,后背端略突伸,覆于后颞骨之上。头部感觉管经后颞骨腹枝,斜穿上匙骨与侧线相连。侧线近沿体轴伸达尾鳍，侧线常骨化成所谓的侧线鳞。匙骨为宽大的圆弧状骨片。后匙骨窄长,略弯曲,紧贴上匙骨和匙骨连接处。锁骨仅在正型标本上部分保存，为一大致呈三角形的骨片。肩带的软骨化骨部分未保存。胸鳍位低，近呈扇形。在 V10998.1—2 号标本上保存有 3—4 枚骨化的辐状支鳍骨(radials of pectoral fin) (图 1,图版 I)。鳍条数目约达 40 根,外侧鳍条略粗，但无棘状鳍条。所有鳍条自近端开始分节,节距长略大于宽,鳍条远端分叉。燕鲟各鳍鳍条的分节情况与软骨硬鳞鱼的较为相似 (Woodward 1895: 图版 I 1)，但明显不同于北票鲟，北票鲟的鳍条节长为节宽的 5—6 倍(刘宪亭和周家健 1965)。

腰带与腹鳍——在现有标本中，腰带部分恰与消化道内容物挤压保存，因而观察不清。腹鳍距臀鳍较胸鳍为近,外形近三角形(图 1)。辐状支鳍骨 (radials of pelvic fin) 一排,共约 10 余枚,鳍条数目约 40 根。

背鳍——在鲟形类所有已知种类中，燕鲟的背鳍极为独特，其背鳍基很长，长可达全长的 1/3 左右。背鳍起点约与腹鳍起点相对,终点则与尾鳍下叶基部棘鳞前端相对。鳍内有两排骨化的辐状支鳍骨，近端一列 (proximal radials of dorsal fin) 41—50 枚,远端一列 (distal radials of dorsal fin) 50—52 枚。鳍条数目 167—176 根，其中前 30 余根往后依次加高。背鳍鳍条和骨化支鳍骨的数目随个体增大而略有增加，如现知三个较完整个体中最小的 V10998.3 号标本,鳍条数目 167 根,近端支鳍骨 41 枚,远端 50 枚;最大的 V10998.1 号标本,则有 176 根鳍条,50 枚骨化的近端支鳍骨,52 枚远端支鳍骨。

臀鳍——臀鳍起点约与背鳍基的前 2/5 处相对,形状与腹鳍相似,但较腹鳍大。鳍内亦有两排骨化的支鳍骨，近端 (proximal radials of anal fin) 20—21 枚，远端 (distal

radials of anal fin) 21—24 枚。鳍条数目 50 余根。

尾鳍——尾鳍为全歪形尾，叉裂浅。尾鳍有 20 余枚骨化的支鳍骨，其数目随个体生长有所增加。尾鳍的支鳍骨包括末端膨大的脉棘 (haemal spines) 和尾下骨(hypurals)，但这两部分的界线在化石上难以确认。此外，尾鳍上叶基部尚保存有 6—7 枚与躯干部上神经棘相似的长形支鳍骨，在此仍沿用 Grande & Bemis (1991) 的上神经棘。尾鳍鳍条 80 余根，但未见轴上鳍条。轴下鳍条由下往上逐渐变细。尾鳍下叶基部有 5—6 对未愈合的棘鳞 (ventral caudal fulcra)；上叶背缘有 20 余对棘鳞 (dorsal caudal fulcra)。最前的尾棘鳞与尾鳍后上方的鳞片极为相似，往后渐变细长。

鳞——除身体两侧各有一列管状侧线鳞外，尾鳍后上方仍保留了数列极为退化的硬鳞，鳞片形状似米粒，已无关节突和凹(图 1，图版 I 1，V10998.6)。

二、比较与讨论

1. 鲟形鱼类的研究现状

鲟形鱼类 (Acipenseriformes) 仅分布于北回归线以北的地区。鲟类最早的化石记录——软骨硬鳞鱼 (*Chondrosteus* Egerton 1858) 发现于早侏罗世海相地层中，但从其近两亿年的地质记录中，发现的种类并不多。除软骨硬鳞鱼外，材料较完整并有系统记述的鲟类化石仅包括单型属列鳍鱼 (*Stichopterus* Reis 1909)、北票鲟 (*Peipiaosteus* Liu et Zhou 1965)、原白鲟 (*Protopsephurus* Lu 1994)、古白鲟 (*Paleopsephurus* MacAlpin 1941) 和齿鳞鲟 (*Crossopholis* Cope 1883)，以及与现生种同属的多瘤匙吻鲟 (*Polyodon tuberculata* Grande et Bemis 1991)。现生鲟类共有六个属：鲟 (*Acipenser* Linné 1758)、鳇 (*Huso* Brandt 1833)、铲鲟 (*Scaphirhynchus* Heckel 1835)、拟铲鲟 (*Pseudoscaphirhynchus* Nikolski 1900)、白鲟 (*Psephurus* Günther 1873) 和匙吻鲟 (*Polyodon* Lacépède 1797)。软骨硬鳞鱼以后的鲟鱼均为淡水性或溯河性鱼类。

鲟形目或软骨硬鳞鱼群 (chondrostean group) 作为低等辐鳍鱼类的一个单系群已为 Jollie (1980)、Patterson (1982)、Gardiner (1984)、Gardiner & Schaeffer (1989) 及 Grande & Bemis (1991) 等的综合性研究工作所确认。目前一般将下列 15 个特征作为鲟形目的裔征：1) 基蝶骨无副基管(含内颈动脉)；2) 动眼肌室退化或消失，开肌窝(容纳腭弓提肌和鳃盖开肌)和下颞窝(鳃盖收肌的起端)缺如；3) 左右腭方骨在前部中线相接，并不与脑颅相关节；4) 舌颌骨扁棒状，间舌骨宽大；5) 鳃弓牙齿限于第一对鳃弓及前两个下鳃骨；6) 吻部骨片退化为众多小骨片；7) 无次眶骨；8) 无前鳃盖骨；9) 鳃盖骨退化；10) 无喉板骨；11) 齿骨未包含下颌感觉管；12) 方颧骨连接腭方骨和上颌骨后端；13) 鳍条上无硬鳞质；14) 体侧鳞片退化为彼此分离的齿状鳞；15) 鳞片无关节突和凹 (Gardiner & Schaeffer 1989: 175—176 页，Grande & Bemis 1991: 106 页)。

鲟形目下属有四个科：软骨硬鳞鱼科 (Chondrosteidae)、北票鲟科 (Peipiaosteidae)、鲟科 (Acipenseridae) 和匙吻鲟科 (Polyodontidae)。鲟科包括鲟、鳇、铲鲟和拟铲鲟四个属，匙吻鲟科有原白鲟、古白鲟、齿鳞鲟、白鲟和匙吻鲟共五个属，这两个科尤其是匙吻鲟科的形态特征和系统关系已较清楚 (Jollie 1980, Grande & Bemis 1991, 卢立伍

1994)。软骨硬鳞鱼科和北票鲟科为化石类群,其中软骨硬鳞鱼、列鳍鱼和北票鲟为三个相对了解较多的属,但它们的形态特征和系统关系仍存在不少问题。

软骨硬鳞鱼发现于英、德两国下侏罗统,为一著名的化石代表,但这一属的研究工作主要完成于上世纪下叶和本世纪初 (Egerton 1858, Traquair 1887, Woodward 1889, 1895, Watson 1925, Hennig 1925)。列鳍鱼和北票鲟的形态非常相似,且两者的产出层位(相当于热河群的地层)基本一致,分布于当时为同一动物地理区的不同地点。前苏联的研究人员(如 Яковлев 1977, 1986) 历来将列鳍鱼归入软骨硬鳞鱼科。刘宪亭和周家健(1965)则以北票鲟为模式属,另行建立北票鲟科。周忠和(1992)对北票鲟的形态特征做了补充和修订,指出体侧有一行侧线鳞、副蝶骨的形态和鳃盖系统的特征等为北票鲟科的主要特征,并建议把列鳍鱼归入北票鲟科。周忠和将列鳍鱼和北票鲟作为一对姊妹属的观点无疑是正确的,但他提出的北票鲟科的前两个特征则并不仅为列鳍鱼和北票鲟所具有。体侧有一列骨化的管状侧线鳞普遍见于匙吻鲟类 (Grande & Bemis 1991); 软骨硬鳞鱼的体侧亦偶见管状侧线鳞 (Woodward 1895: 29 页),但骨化程度可能较低;鲟科鱼类的身体侧骨板中则含有侧线鳞(据笔者观察, Jollie 1980)。副蝶骨的形态虽在软骨硬鳞鱼中不清楚,但是所有其它鲟形鱼类副蝶骨的形态结构与北票鲟的基本一致,唯匙吻鲟类的副蝶骨随头骨伸长而变细长 (Яковлев 1977, Grande & Bemis 1991)。周忠和提出的北票鲟科的鳃盖系统特征则为一复合性状,意义不够明确。软骨硬鳞鱼的鳃盖骨相对下鳃盖骨已很小,下鳃盖骨后缘光滑,长条状鳃盖骨 8—10 对 (Woodward 1889, Watson 1925: 图 8);鲟科鱼类已无鳃盖骨,下鳃盖骨未特化,但只有 1—3 对形状复杂的鳃条骨 (Jollie 1980); 匙吻鲟类的下鳃盖骨后部裂成棒状,鳃条骨 1 对 (Grande & Bemis 1991)。列鳍鱼和北票鲟的鳃盖骨比软骨硬鳞鱼的更为退化,下鳃盖骨后部仅裂成片状,鳃条骨不超过 7 对,但形状已趋于复杂。由此可见,列鳍鱼和北票鲟鳃盖系统的形态特征处于从软骨硬鳞鱼到现生鲟类的过渡阶段,作为一个性状则与上下类群镶嵌具有。因此,软骨硬鳞鱼等早期鲟类化石仍有待“详细的解剖学和系统学研究”(Grande & Bemis 1991: 116 页)。

2. 燕鲟系统位置的初步分析

在燕鲟的现有标本中,可观察到上述鲟形目裔征中的 11 个(特征 3、4、6、7、8、9、10、11、12、14、15);特征 1、2、5 及 4 的间舌骨在标本中未保存,因而情况不明;特征 13 在燕鲟中为原始状态,燕鲟的膜质骨和鳍条上均被有硬鳞质层,已知鲟类中仅软骨硬鳞鱼的部分头骨上残留有硬鳞质层 (Gardiner 1984)。由于早期的化石种类往往保留更多的原始特征,如软骨硬鳞鱼尾叶上的鳞片仍具有正常的关节突和凹,因而笔者认为燕鲟无疑可归入鲟形目。

在鲟类已知属种中,燕鲟与软骨硬鳞鱼、列鳍鱼和北票鲟三个属有不少相似之处(参见本文图 1—3,周忠和 1992, Яковлев 1977, Traquair 1887): 1) 头骨吻短而圆钝,不明显前伸; 2) 颅顶骨骼的组成和形态; 3) 肩带膜质骨骼的特征; 4) 腭方骨厚大,半圆形; 5) 外翼骨钩状,与上颌骨中部相接; 6) 上下颌、舌弓、鳃弓及鳃耙的形状; 7) 退化的鳃盖骨; 8) 体侧有一行管状侧线鳞。燕鲟与软骨硬鳞鱼的相同点: 1) 体型较侧扁;

2）膜质头骨上残留有硬鳞质层；3）各鳍鳍条分节密，节长略大于节宽；4）尾上叶有鳞片，但不如软骨硬鳞鱼发育，且无关节突和凹（列鳍鱼亦有尾部鳞片）；5）尾上叶棘鳞发育，几覆盖整个上叶背缘。燕鲟与列鳍鱼和北票鲟的共同点：1）吻部骨片退化为管状或形状不规则的小骨；2）下鳃盖骨前中部向前舌状突出，后部裂成锯齿状；3）尾鳍叉裂浅。燕鲟与软骨硬鳞鱼、列鳍鱼和北票鲟三属的主要区别：1）有骨化的腭骨；2）方颧骨长条形；3）眶上、眶下和眶后感觉管在膜质蝶耳骨上相连（这一特征在软骨硬鳞鱼上情况不明）；4）椎体弓片、上神经棘、肋骨和各鳍支鳍骨等的骨化程度高；5）有一很长的背鳍，背鳍基长可达全长的 1/3；6）各鳍鳍条上被有硬鳞质；7）尾鳍无轴上鳍条，尾下叶基部有 4—6 对未愈合的棘鳞。

从以上粗略的比较可以看出：1）燕鲟和软骨硬鳞鱼等早期鲟类化石的头骨形态结构基本一致，属鲟形鱼类的原始状态。2）燕鲟和软骨硬鳞鱼的体型较侧扁，头骨上残留有硬鳞质层，显示比列鳍鱼和北票鲟更多的原始性；3）燕鲟同时与列鳍鱼和北票鲟具有一些比软骨硬鳞鱼进步的特征，如吻部骨片退化为形状不规则的管状小骨，下鳃盖骨前部明显呈舌状突出，后部裂成锯齿状。根据上述分析，笔者认为燕鲟应处于比软骨硬鳞鱼进步但比列鳍鱼和北票鲟原始的位置，很可能为列鳍鱼和北票鲟的近祖姊妹属，暂将其归入北票鲟科。北票鲟科目前只发现二三点不为鲟形目其它类群所具有的特征：1）吻部由管状小骨片组成；2）鳃条骨 4—6 根；3）尾鳍上的硬鳞退化或消失。

有关鲟形鱼类的系统关系综合起来有两种观点：一种以 Gardiner（1984：图 2）和周忠和（1992：图 8）为代表，认为鲟类的演化分为两支，一支以匙吻鲟科为代表，另一支包括软骨硬鳞鱼科、北票鲟科和鲟科；第二种观点由 Grande & Bemis（1991：图 76B）提出：将鲟类的发展作为一个序列。对第一种观点，Grande & Bemis（1991）文中已逐条评述了 Gardiner 提出的两个分支的特征，认为大多含义不清或分布范围有误。周忠和曾列出腭翼骨、方颧骨和眼后腹缘眶下骨的形状，以及齿骨上感觉管完全消失共四点特征为软骨硬鳞鱼科—北票鲟科—鲟科这一分支的裔征。Grande & Bemis 亦讨论了这四个特征中的三个（周的特征大多引自 Patterson 1982），发现鲟科鱼类的腭翼骨形状更接近于原始的匙吻鲟类；方颧骨应为整个鲟形目的特征；眼后腹缘呈直角形的宽大眶下骨则可能表示了软骨硬鳞鱼科和鲟科之间的关系。笔者认为周提出的方颧骨镰刀形确为软骨硬鳞鱼科至鲟科这一分支所特有，但这一特征有无可能属原始状态仍有待证实；北票鲟和燕鲟眼后腹缘眶下骨的形状则不同于软骨硬鳞鱼和鲟，而与匙吻鲟类的管状骨相似；齿骨上感觉管在鲟科中完全消失，在匙吻鲟类中亦很退化，但有无这一特征在化石上很难确认，如属匙吻鲟类的古白鲟和原白鲟就未见有齿骨感觉管的记述（MacAlpin 1947, Grande & Bemis 1991, 卢立伍 1994）。因此，支持鲟形鱼类分为两大支的许多特征仍有待观察更多的标本，尤其是化石材料去确证。至于 Grande & Bemis 提出的鲟类系统关系的第二种观点，笔者认为所引用的形态特征及其分布范围与目前对化石和现生鲟类的了解基本一致。北票鲟科尚不具鲟亚目（鲟科+匙吻鲟科）的特征（Grande & Bemis 1991：特征 7—10），但起码以鳃条骨数目少于 7 根和尾鳍上硬鳞无关节突和凹等特征比软骨硬鳞鱼进步，因此可将其视为鲟亚目的近祖姊妹群。本文第一作者将在《冀北辽西的鲟类化石及其在系统关系上的意义》一文中对燕鲟、北票鲟和原白鲟等作进一步的形态特征和系统关

系分析。

3. 燕鲟的地理分布和生存时代

燕鲟最初发现于河北北部丰宁县森吉图乡义县组地层中，古脊椎所鱼类室中生代组在辽宁西部凌源、朝阳等地的义县组地层中也发现了不少的燕鲟标本。相信随着工作的深入和燕鲟的报道，将在冀北辽西和内蒙东部地区的更多地点发现这一类化石。燕鲟与北票鲟一样，也将成为热河动物群的重要成员。

燕鲟的生存时代即热河动物群的时代，这是一个争论了半个多世纪的问题。笔者认为以往的不少争论源于概念混淆或囿于已见，如不少文章将岩石、生物和年代地层学三者混为一谈，试图单纯依据所谓的标准化石或化石组合去划分千变万化的陆相地层并确定其年代，其实对陆相盆地而言，这三者的界线往往是不一致的。限于此文篇幅，笔者将另文讨论现代地层学的概念与热河动物群时代的确定。在此，笔者虽基本同意李佩贤等(1994)在《狼鳍鱼（*Lycoptera*）岩层的时代归属》一文中对近年来获得的许多新资料的综合分析和讨论，但认为尚缺乏足以使人信服的证据表明整个含狼鳍鱼岩系应划归白垩系。因此，燕鲟的生存时代为晚侏罗世或早白垩世仍有待进一步的研究工作去确定。最后，简介一点有关热河群的新认识：1）九佛堂组和义县组以往视为上下两个不同年代的地层单元，但笔者认为这是两个基本同期的岩石地层组，属同期异相沉积。这一认识的依据为区域地层发育序列、构造火山活动的迁移、沉积相和生物组合。2）九佛堂组和义县组的沉积速率很大，沉积这一厚达几千米的岩层延续的时间远比以前估计的要少，这一点主要是根据沉积韵律和顶底火山岩的同位素年龄。

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AN EARLY FOSSIL STURGEON (ACIPENSERIFORMES, PEIPIAOSTEIDAE) FROM FENGNING OF HEBEI, CHINA

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Key words Fengning, Hebei, Late Jurassic or Early Cretaceous, Fossil Sturgeons

Summary

During a field work on stratigraphy Mr. Yang Youshi *et al.*, the geologists from the Regional Geology and Mineral Resources Survey Institute of Hebei Province, discovered some well-preserved fossil sturgeons from the Yixian Formation in Fengning County, northern Hebei Province. These specimens, characterized by an extraordinarily long dorsal fin, represent a new form *Yanosteus longidorsalis* gen. et sp. nov. of the order Acipenseriformes. *Yanosteus* is stratigraphically concurrent with two known acipenseriform genera—— *Peipiaosteus* Liu et Zhou and *Protopsephurus* Lu in northern Hebei and western Liaoning. The fishbearing strata of Yixian Formation have long been thought to be Late Jurassic (Liu & Zhou 1965, Lu 1994), but additional evidence suggests an Early Cretaceous age (Li *et al.* 1994).

Order Acipenseriformes Berg, 1940
Family Peipiaosteidae Liu et Zhou, 1965
Genus *Yanosteus* gen. nov.

Generic diagnosis Acipenseriform with extremely elongated dorsal fin (length of its base about 1/3 of total body length). The taxon differing from other genera of Peipiaosteidae in possessing ossified palatine; splint-like quadratojugal; supraorbi-

tal, infraorbital and postorbital sensory canals connected in dermosphenoid; vertebral arcuales, supraneurals, pleural ribs and pterygiophores well-ossified; ganoine present on fin rays; no caudal fin rays dorsal to notochord; and ventral margin of caudal fin proceeded with a few pairs of fulcra.

Etymology Yan—— abbreviation for northern Hebei Province in Chinese phonetic alphabet where the specimens were discovered; osteus——after Greek "osteon", meaning bone, which is popular with the generic names of primitive fossil sturgeons.

Type and only species *Yanosteus longidorsalis* sp. nov.

Yanosteus longidorsalis gen. et sp. nov.

(Figs. 1—2; Pls. I—II)

Specific diagnosis As for genus. Head length (from anterior tip of snout to posterior end of subopercle) about 1/5 of total length; numbers of fin rays: pectoral and pelvic about 40, dorsal 167—176, anal a few more than 50, and caudal nearly 90; more than 20 pairs of dorsal fulcra and 4—6 pairs of ventral fulcra present on caudal fin; caudal scales constricted to rear part of upper caudal lobe, and devoid of peg-and-sockets.

Type specimen A complete fish, catalogue number of IVPP: V10998.1.

Referred specimens Two nearly complete individuals (IVPP V10998.2—3), two incomplete skulls and a caudal specimen (IVPP V10998.4—6).

Locality, horizon and age Dongtuyao, Senjitu, Fengning County, Hebei Province; Yixian Formation; Late Jurassic or Early Cretaceous.

Etymology Longi—— after Latin "longus", long; dorsalis ——after modern Latin "dorsalis", dorsal. The specific name refers to the long dorsal fin.

Description The total length of the specimens described in this paper ranges from about 270mm to 460mm (the smallest and largest individuals represented by the incomplete skull V10998.5 and the caudal specimen V10998.6), and the holotype V10998.1 measures 454mm TL. The skeleton of *Yanosteus* is better-ossified compared with previously known extinct and Recent acipenseriforms, and the dermal bones and fin rays have remnants of ganoine.

The head is relatively short, its length from the anterior tip of snout to the posterior end of subopercle attaining 1/5 of the total length. In the present specimens, the skulls are all preserved in dorso-lateral aspect which indicates the body of *Yanosteus* is not so ventrally depressed as *Peipiaosteus* and extant acipenseriforms (Fig.1; Pls.I, II 1), *Peipiaosteus* often preserved in dorso-ventral aspect.

Yanosteus bears a strong resemblance to *Chondrosteus* and *Peipiaosteus* in the cranial skeleton. In all three genera, the rostrum is not prominent and the anterior end of jaws is only slightly behind the tip of snout. The greatly protruding rostrum and posteriorly located mouth of *Chondrosteus* in Traquair's (1887) and Watson's (1925) restorations is mistakenly made possibly influenced by the elongated rostrum in extant sturgeons and paddlefishes. The rostrum in *Yanosteus* and *Peipiaosteus* is supported by a series of tube-like or irregular-shaped ossicles including nasal, rostral, and front infraorbital bones (Figs.1—2, Zhou 1992: Fig.1).

The elongate frontal, parietal and dermopterotic are the main plate bones of the skull roof. The dermosphenoid is inserted between the frontal and dermopterotic, and the supraorbital, infraorbital and postorbital sensory canals connect in this bone (Figs. 1—2, IVPP V10998.6). The posttemporal of both *Yanosteus* and *Peipiaosteus* is a fork-like bone, while the ventral branch is rather slim (Figs.1, 3B). Zhou (1992: Fig.3) incorrectly identified the posttemporal in *Peipiaosteus* as the upper part of supracleithrum. The triradial bone bearing the supratemporal canal should be the extrascapular. On the ventral side of neurocranium, the only preserved bone is the large parasphenoid, which is similar to that of *Peipiaosteus* (Fig. 2A, Liu & Zhou 1965: Fig.2A). Around the eye posteroventrally is a series of tube-like infraorbital bones (about 5—6 in number), however no large right-angled infraorbital is observed among this series in the present specimens. The palatoquadrate (=pterygoid of Woodward 1895, palatopterygoid of Zhou 1992), ectopterygoid or ectopterygoid process of maxilla (=palatine of Woodward 1895), maxilla and dentary of the jaws in *Yanosteus* also resemble the corresponding elements in *Chondrosteus* and *Peipiaosteus*. In front of the palatoquadrates in *Yanosteus*, there is a pair of bones with concentric growth lines in them, and they may be the palatines just as those developed in some adults of *Paleopsephurus* and extant acipenseriforms (MacAlpin 1947, Jollie 1980, Grande & Bemis 1991). The quadratojugal in *Yanosteus* is splint-shaped, slightly different from the sickle-like bone in *Peipiaosteus* etc. (Zhou 1992: Fig.7). Of the hyoid and branchial arches, some flattened rod-like bones and gill rakers are exposed between the jaws and the pectoral girdle (Figs.1—2). In the opercular series, *Yanosteus* is more similar to *Peipiaosteus* than to *Chondrosteus*. The opercle of *Yanosteus* and *Peipiaosteus* is further reduced to an elliptical ossicle. The subopercle is a large semicircular bone with its posterior margin ctenoid and with a developed tongue-like process on the anterior margin. Besides some fragments, no complete branchiostegal is preserved in the present specimens.

The vertebral column of *Yanosteus* consists of about 50—55 vertebrae excluding those in the caudal fin. There are only ossified basidorsals in the precaudal region, and basidorsals plus basiventrals in the caudal region (Fig.1). No ossified interdorsals or interventrals are preserved in all available specimens. In the three complete specimens (V10998.1—3), there are about 10 pairs of the anteriormost pleural ribs ossified. The supraneural series in *Yanosteus*, unlike those in polyodontids, is interrupted under the dorsal fin, which is inconsistent with the viewpoint of Grande and Bemis (1991) that there is a continuous uninterrupted series of supraneurals in Acipenseriformes. The condition of a continuous supraneural series may be restricted to polyodontids among acipenseriformes.

The dermal pectoral girdle of *Yanosteus* also closely resembles those of *Chondrosteus* and *Peipiaosteus* (Figs. 1—3). The supracleithrum is a nearly oval-shaped bone with its elongated upper extremity overlapping the posterior end of posttemporal, and with the lateral line obliquely crossing it. The cleithrum is a robust bone with a greatly expanded inner laminar, in front of which is the triangular clavicle. Behind the joint of the supracleithrum and cleithrum lies the small splint-like postcleithrum. The pectoral fin contains about 40 fin rays, which

are closely articulated starting from the proximal end and branched distally. In the specimens V10998.1—2, 3—4 radials of the pectoral fin are ossified. The pelvic fin is situated closer to the anal fin than to the pectoral fin, and also contains about 40 fin rays. The pelvic fin is supported by one row of more than 10 ossified radials.

The dorsal fin is unique among the known acipenseriforms, for it consists of 167—176 fin rays and its base length is about 1/3 of the total body length. The dorsal fin is supported by two rows of ossified pterygiophores, the proximal row having 41—50 radials and the distal 50—52 radials. The anal fin consists of a few more than 50 fin rays, and is also supported by two series of pterygiophores, the proximal series having 20—21 ossified radials and the distal 21—24 radials.

The caudal fin is heterocercal and only slightly forked. The caudal fin contains nearly 90 fin rays but have no fin rays dorsal to the notochord, which are supported by the distally expanded haemal spines and hypurals. On the dorsal margin of the upper caudal lobe, there are more than 20 pairs of unfused fulcra. Under the base of the fulcra there are 6—7 pterygiophores (=supraneurals of Grande & Bemis 1991). The ventral margin of the lower caudal lobe is proceeded with 4—6 pairs of fulcra.

The lateral line extends posteriorly from the supracleithrum to the caudal fin along the way parallel to the notochord, and the lateral line canal is often ossified as the so-called lateral line scales (Liu & Zhou 1965, Zhou 1992). The caudal scales are constricted to the rear part of the upper caudal lobe, and devoid of peg-and-sockets.

Remarks *Yanosteus* has the following characters which are thought to be derived for Acipenseriformes (Gardiner & Schaeffer 1989): (1) palatoquadrate with an anterior symphysis, and not articulating with neurocranium; (2) hyomandibular large, blade-shaped; (3) rostral bones reduced, numerous; (4) suborbital bones absent; (5) preopercle absent; (6) opercle reduced; (7) gulars absent; (8) dentary without enclosed mandibular canal; (9) body scaling reduced to isolated denticles; (10) scutes devoid of peg-and-socket. In the characters listed by Grande and Bemis (1991) for Acipenseriformes also includes quadratojugal linking palatoquadrate with posterior end of maxilla. Although most of these characters need to be verified in the future study, it is no doubt to assign *Yanosteus* to the order Acipenseriformes.

Among the known genera of this order, *Yanosteus*, on the one hand, resembles *Chondrosteus* in the characters of body form, rostrum, skull roof, palatoquadrate, ectopterygoid, opercle, dermal pectoral girdle and lateral line scales etc., however most of which are general or primitive to Acipenseriformes. On the other hand, *Yanosteus* is similar to *Peipiaosteus*, and probably also to *Stichopterus* in having rostral bones reduced to tube-like ossicles, subopercle with a ctenoid posterior margin and with a developed tongue-shaped process on anterior margin, and scales in caudal fin reduced and devoid of peg-and-socket, which are also the main characters of Peipiaosteidae. Hence, *Yanosteus* is more closely related to *Peipiaosteus* than to *Chondrosteus*, and most likely belongs to the family Peipiaosteidae.

Zhou (1992) redefined the family Peipiaosteidae (***Peipiaosteus*** + ***Stichopterus***) with three characters: lateral line scales, opercular series, and shape of parasphenoid. But none of Zhou's features are unique to peipiaosteids. The ossified lateral line canals (= scales of Zhou) are present in all acipenseriforms including ***Chondrosteus*** (Woodward 1895, Jollie 1980, Grande & Bemis 1991); the opercular series is a complex character, and the condition in Peipiaosteidae is morphologically intermediate between Chondrosteidae and Acipenseroidei sensu Grande et Bemis; and the shape of the parasphenoid is also ambiguous, in fact the parasphenoid in acipenseriforms is basically constructed in the same pattern, except in polyodontids it is greatly elongated in accordance with the extension of the skull. A concise diagnosis of Peipiaosteidae is still waiting for a critical review of the included members. For the time being, the following characters seem to unite ***Yanosteus***, ***Peipiaosteus*** and ***Stichopterus*** within Peipiaosteidae: rostral bones reduced to tube-like ossicles, branchiostegals 4—6 in number (this condition is presently unknown in ***Yanosteus***, but its number should not exceed this range), and scales in caudal fin greatly reduced or absent.

On the phylogenetic relationships of Peipiaosteidae, Zhou (1992: Fig. 8) proposed a cladogram basically similar to the tree of Acipenseriformes of Gardiner (1984: Fig. 2), but he correctly placed ***Paleopsephurus*** as the sister group of ***Polyodon*** and concluded that ***Peipiaosteus*** is closer to ***Acipenser*** than to ***Chondrosteus***. No conclusion is to be given on the interrelationships of Acipenseriformes in this paper. However, it should be pointed out that Zhou's characters 1—4 of the group (***Acipenser*** +Peipiaosteidae)+***Chondrosteus*** are questionable. The sickle-like quadratojugal in this group may be of primitive state which is modified in most polyodontids. The large and right-angled infraorbital posteroventral to the orbit in Chondrosteidae and Acipenseridae is not developed in ***Peipiaosteus*** and ***Yanosteus***, instead, this bone is more like the tube-shaped infraorbital in polyodontids. The mandibular sensory canal is rarely preserved in fossils. Except in ***Crossopholis***, no records have been made on this character in fossils including those belonging to Polyodontidae. As for the last character of Zhou's, Grande and Bemis (1991) mentioned that "the 'form' of the palatopterygoid in sturgeons is closer to that of primitive polyodontids than to that of Chondrosteidae". So, the Chondrosteidae+(Peipiaosteidae+Acipenseridae) as a monophyletic group is still lack of characters to support. The number of branchiostegals no more than 7 and the scales in the caudal fin devoid of peg-and-sockets may be the derived characters for a group (Peipiaosteidae+Acipenseroidei) minus Chondrosteidae. A phylogenetic analysis of ***Yanosteus*** and related forms is being carried out by the first author of this paper.

图版说明 (Explanations of plates)

图 版 I

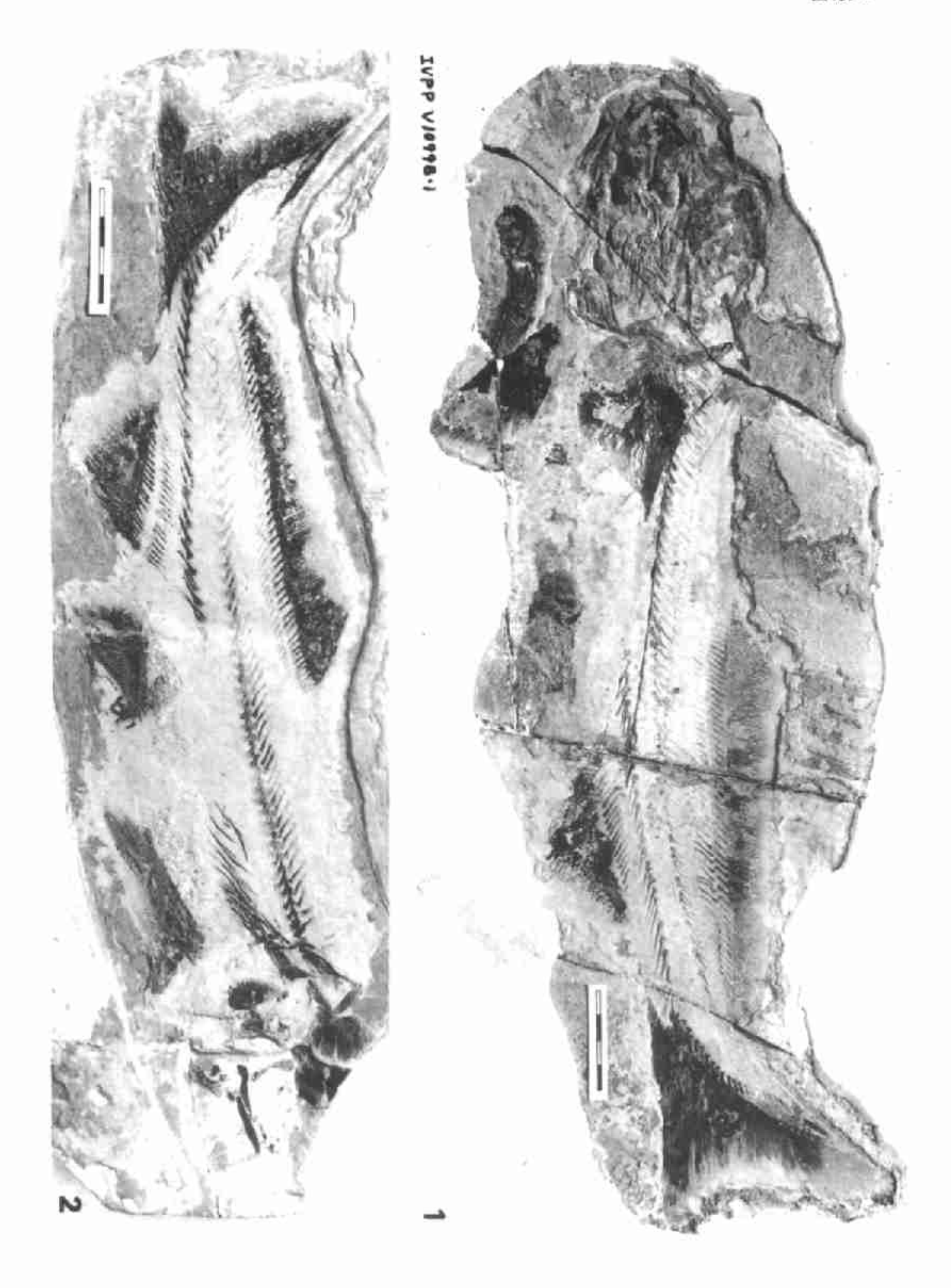
长背鳍燕鲟(新属新种) 1) 正型标本左侧视，V10998. 1; 2) 一近完整标本(颅顶前部略有缺失)右侧视，V10998.2

Yanosteus longidorsalis gen. et sp. nov. 1) Holotype (IVPP V10998.1, 454mm TL) in left lateral view; 2) a nearly complete specimen (IVPP V10998.2, 394mm TL) in right lateral view

图 版 II

长背鳍燕鲟(新属新种) 1) 一近完整标本(胸鳍缺失)右侧视，V10998.3; 2) 一不完整的头骨(缺失后端)背—侧视，V10998.4; 3) 头部骨片背—侧视，V10998.5

Yanosteus longidorsalis gen. et sp. nov. 1) A nearly complete specimen (IVPP V10998.3, 334mm TL) in right lateral view; 2) an incomplete skull(IVPP V10998.4) in dorso-lateral view, anterior toward left; 3)part of skull skeleton(IVPP V10998.5) in dorso-lateral view


IVPP V10998·1
1
2

